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# Two-Joint Muscles Offer the Solution, but What Was the Problem?

*Maarten F. Bobbert and A.J. "Knoek" van Soest*

Prilutsky's paper is mainly concerned with the coordination of one- and two-joint muscles. This commentary on the paper addresses the question why we have two-joint muscles in the first place. From an evolutionary point of view, two-joint muscles must have contributed to fitness by presenting a solution to problems that could not be solved with musculoskeletal systems comprising only one-joint muscles. One such problem, not mentioned by Prilutsky, is the following. In a system equipped with only one-joint muscles, satisfying directional constraints would demand, in certain phases of movements, deactivation of muscles that are shortening. Consequently, the work output of these muscles would be limited. The incorporation of two-joint muscles helps to overcome this problem. The reason is that it offers the possibility to redistribute energy across joints, thereby making it possible to accomplish more successfully the difficult task of producing work while steering the movement.

**Key Words:** human movement, muscle function

## Introduction

Prilutsky starts his nice paper by noting that the activation of individual limb muscles in skilled motor tasks appears to have stereotyped features despite the redundancy of the motor system. This has motivated investigators to search for optimization criteria predicting the basic features of stereotypical muscle activation and to explain why this specific activation has been selected through evolution and learning. In his paper, Prilutsky concentrates on the coordination of two- and one-joint muscles. He first identifies those features of coordination of major one- and two-joint muscles that are shared among different static and dynamic tasks. Subsequently, he demonstrates that these features can be qualitatively predicted from measured joint moments using static optimization to minimize the sum of muscle stresses cubed. Finally, he addresses the functional consequences of the observed muscle coordination.

We feel that before investigating the coordination of two- and one-joint muscles, one should ask the question why we have two-joint muscles in the first

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place. After all, design of the musculoskeletal system is also one of the outcomes, if not the primary outcome, of evolution. Although neural circuitry specifying elementary coordination patterns may have co-evolved with the musculoskeletal system, we feel that most of the intricacies of coordination are secondary to design and are acquired through learning in higher animals. In this commentary, we shall first argue that, with the real musculoskeletal system comprising two-joint muscles, greater performance may be achieved in certain tasks than with a system in which the two-joint muscles are made mono-articular or replaced by sets of two one-joint muscles. This is because two-joint muscles help to solve a crucial problem not mentioned by Prilutsky. Secondly, we will address the question whether the existence of two-joint muscles simplifies control of the musculoskeletal system. The ideas expressed in this commentary are not new. They have been expressed by Gerrit Jan van Ingen Schenau and his coworkers in various papers. Unfortunately, it seems that the ideas and their implications have not been fully understood. By slightly reformulating them we hope to change that.

### Two-Joint Muscles and Maximum Performance in High-Energy Tasks

The presence of two-joint muscles is one of the most puzzling design aspects of the musculoskeletal system. Let us focus on the lower extremity to explain why it is puzzling. In basic locomotor activities such as walking, running, and jumping, the lower extremity is either shortening or lengthening. Shortening (e.g., upon landing from a jump) typically involves a combination of hip flexion, knee flexion, and dorsiflexion at the ankle, whereas lengthening (e.g., during a push-off) typically involves a combination of hip extension, knee extension, and plantar flexion (see, for instance, Figure 8 of Prilutsky's paper). During these combinations of joint rotations, the major two-joint muscles such as hamstrings, m. rectus femoris, and m. gastrocnemius are simultaneously producing at one joint a moment in the same direction as the angular motion, and at the other joint a moment in the direction opposite to the angular motion.

For instance, during extension of the lower extremity in jumping, plantar flexion and knee *extension* occur simultaneously while m. gastrocnemius is producing a plantar flexion moment and a knee *flexion* moment. What is the use of the action at the knee? At first glance, it seems counter-intuitive to generate a moment opposite to the ongoing angular joint motion, but perhaps intuition is wrong. After all, from an evolutionary perspective two-joint muscles should be considered the solution to problems. In other words, musculoskeletal systems equipped with two-joint muscles must have been fitter than systems with only one-joint muscles. In the search for problems solved by two-joint muscles, one would like to perform "experimental anatomy": One would like to investigate in specific tasks how making a two-joint muscle mono-articular, or replacing it by a set of two one-joint muscles, affects maximum performance. For obvious reasons this cannot be done *in vivo*, and therefore researchers have turned to forward simulation studies with a model of the musculoskeletal system. In such studies, maximum performance can be found by optimization of the stimulation-time input of the muscles. This way, the effect of design aspects on maximum performance can be studied.

To date, such studies have only been conducted for vertical jumping, where performance can be unambiguously defined as maximum height achieved by the

center of mass. Specifically, the question in these studies (Bobbert & van Zandwijk, 1994; Pandy & Zajac, 1991; van Soest et al., 1993) was how maximum jump height changed when m. gastrocnemius was turned into a mono-articular plantar flexor, so that it could no longer produce a knee flexion moment during knee extension. According to the results, evolution was right and intuition wrong: Maximum jump height was greater with m. gastrocnemius as a two-joint muscle than with m. gastrocnemius turned into a one-joint plantar flexor, albeit by a few centimeters at most (Bobbert & van Zandwijk, 1994; van Soest et al., 1993).

The next question is, of course, *why* a greater maximum performance may be achieved with two-joint muscles than with only one-joint muscles. That brings us to the unique action of two-joint muscles. To explain this action and its utilization, we first need to realize that for maximization of performance, it is not sufficient to maximize the total work output of all muscles; directional constraints also need to be satisfied (e.g., Bobbert & van Ingen Schenau, 1988; van Ingen Schenau 1989). During the push-off in vertical jumping, hip extension, knee extension and plantar flexion occur. Thus, we know that the mono-articular hip extensors, knee extensors, and plantar flexors shorten. To maximize their work output, they should produce as much force as possible during shortening. However, their forces contribute to the net joint moments, and *these net joint moments need to be precisely tuned to satisfy directional constraints*; after all, they are driving the body segments and therewith cause the intended movement.

For instance, during the last part of the push-off, the knee is extending, but unfortunately, because of the configuration of the system, steering the center of mass in the vertical direction requires a reduction of the knee joint moment from large extension values to zero and even to flexion values. This means that in order to satisfy the directional constraint, the knee extensors have to be deactivated, so that part of their shortening range is traveled at submaximal force and a submaximal amount of work is produced, and/or a knee flexor muscle has to be activated. If the knee flexor were a one-joint muscle, it would simply dissipate energy produced by the knee extensors. In reality, the knee extensors remain active and the net knee extension moment is reduced by activation of the two-joint m. gastrocnemius, which does not necessarily dissipate energy. After all, if m. gastrocnemius remains at the same length while the knee is extending, the energy produced by the knee extensors is not dissipated but appears as ankle joint work. (It may be said that the energy is transported from proximal to distal in an approach in terms of net joint variables, as opposed to an analysis in terms of segmental energies used by Pandy & Zajac, 1991).

Cleland (1866) called this action of m. gastrocnemius "ligamentous action" and realized that it allowed the knee extensors to indirectly act on the ankle joint. In a net joint work approach, it may be said that m. gastrocnemius transfers work produced by the knee extensors to the ankle joint. *The essence of the mechanism is that the knee extensors may continue to produce work even if the directional constraints require a small knee extension moment or a knee flexion moment.* If m. gastrocnemius shortens during knee extension, it not only allows the knee extensors to continue their work production without violating directional constraints, but also adds energy itself. If it lengthens, it still allows the knee extensors to continue their work production, but at the same time it dissipates energy. Even in that case, however, the balance may be positive so that activation of m. gastrocnemius still has a beneficial effect on performance. At first glance, one may not

expect that a relatively small muscle like *m. gastrocnemius* is able to counteract the much larger knee extensor muscles. However, because of the simultaneous knee extension and plantar flexion, the contraction velocity of *m. gastrocnemius* remains low so that it operates in a more favorable part of its force-velocity relationship than the knee extensor muscles and consequently may produce a greater relative force.

Above, it has been argued that if *m. gastrocnemius* were a one-joint plantar flexor, a problem would arise at the knee joint during the push-off in jumping: For maximization of the amount of work produced, one would like to keep the knee extensors maximally activated over their full shortening range, but this would violate directional constraints; these constraints dictate that the knee extensors be deactivated before they have fully shortened. Obviously, in a system equipped with only one-joint muscles, this problem would occur not only at the knee joint during jumping. It would be a general problem occurring at joints in all tasks involving propulsion of the center of mass relative to the environment or propulsion of objects in the environment relative to the body using the hand or the foot. Fortunately, in the real system, the problem may be solved by virtue of the unique energy-transferring action of two-joint muscles. At this point, the reader may argue that if muscles are deactivated during shortening, it is in *submaximal* tasks not detrimental to performance. However, deactivating muscles during shortening does not solve the so-called conflict situations (van Ingen Schenau, 1989) where directional constraints require a flexion moment while the joint is extending or an extension moment while the joint is flexing. In a system with only one-joint muscles, solving such conflicts involves energy dissipation, but fortunately, in the real system, the conflicts can be solved without energy dissipation by activating two-joint muscles. This obviously benefits efficiency and endurance. We would therefore speculate that the unique energy redistributing action of bi-articular muscles makes it possible to accomplish more successfully the difficult task of producing work while steering the movement, and therefore has contributed to the fitness of animals in evolution. Admittedly, it is not the only advantage. Prilutsky mentions another important advantage that was already identified by Cleland (1866): Locating the powerful muscles proximally and transferring the energy produced distally via the “ligamentous action” of the two-joint *m. rectus femoris* and *m. gastrocnemius* helps to minimize the moment of inertia of the limbs and, therewith, metabolic energy consumption.

## Two-Joint Muscles and the Organization of Control

Above, it has been argued that net moments at the different joints must be precisely tuned to satisfy directional constraints. In a system with only one-joint muscles, this would limit the amount of work that can be produced. In the real system, however, two-joint muscles may redistribute energy output among joints. This has led to the hypothesis that one-joint muscles are only concerned with work production, while two-joint muscles are concerned with the tuning of net joint moments needed to satisfy directional constraints (van Ingen Schenau et al., 1992). This would imply that control of a system with two-joint muscles is simpler and more flexible than control of a system with only one-joint muscles. Moreover, it was hypothesized that in high-energy tasks, the activation of one-joint muscles could be based only on muscle spindle information (the muscles should be activated

when shortening and silent when lengthening) while that of two-joint muscles could be based on various other types of sensory information, among which information on the intersegmental dynamics and information about the line of action of the forces exerted on the environment (van Ingen Schenau et al., 1994). Unfortunately, to date no convincing support for these hypotheses on the organization of control has been found in experiments on human subjects (Doorenbosch et al., 1997), most likely because joint moments and work production cannot be controlled completely independently. The reason is that by changing the force of a two-joint muscle, one cannot adjust the moments at the joints spanned by this muscle independently. Thus, to satisfy directional constraints, the forces of one-joint muscles may need to be adapted as well. At this point in time, it cannot be said whether the unique action of two-joint muscles may be exploited to simplify control. Hopefully, future (simulation) studies will shed more light on this issue.

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Gerrit Jan van Ingen Schenau played a crucial role in the development and experimental pursuit of the ideas summarized briefly in this commentary. We are sure that he would have presented them more convincingly, but nevertheless hope that the commentary does justice to the ideas. We very much regret that we can no longer ask Gerrit Jan whether this is so.